THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

VOL. 76 JANUARY, 1959 NO. 1

AN APPROACH TO THE STUDY OF MOLTS AND PLUMAGES

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1. INTRODUCTION

During the course of studies of the molts and plumages of certain waterfowl and other birds, it has become apparent to us, as it has to a number of other workers, that the description of plumage successions has often been hampered by the lack of a uniform and practical terminology. It was our original intent to introduce a new terminology applicable, as far as possible, to all birds, in order to eliminate some of the semantic difficulties of the past. As this project progressed, it became obvious that knowledge of the plumage stages of many species is sadly incomplete or poorly understood; further study revealed the need of a reexamination of many long-held concepts of plumage succession and of more precise definitions of widely but ambiguously used terms. The subject is too large to be covered in a single paper. We propose here to discuss plumage succession beginning at the time of loss of the juvenal plumage, i.e., the bird's first covering of true (in some cases modified) contour feathers. We hope in a later paper to analyze the development of the plumages from the embryo through the completed juvenal plumage. We have adopted this reversed chronological sequence because of the complexity of the question of the "natal downs" and their origin, which we intend to investigate at some length.

We hope in this paper to throw new light on concepts of plumage and molt, and we present a framework within which descriptive and comparative studies may be made. In spite of the vast progress made by many workers in recent decades in understanding some of the factors which affect the physiology of molt (genetic control, hormonal balance, photoperiod, temperature, diet, etc.), it must be remembered that such information is available for but a small fraction of the species of birds of the world. We believe it is greatly desirable to have

a system available whereby variations in the patterns of plumage succession may be described, compared, and contrasted among different groups of birds, whether or not the physiological mechanisms have been worked out for the groups in question.

In reviewing the recent literature in which intrinsic and extrinsic factors affecting molt have been discussed, it has become apparent that such factors may vary widely in relative importance among different groups of birds. In striking contrast to this heterogeneity is what appears to be a fundamental pattern of plumage succession which can be traced almost throughout the class Aves. Such a pattern has been noted and utilized by students of this subject for over a century. The prevalence of this apparently consistent pattern leads us to believe that a broad concept of homology, such as that advocated by Hubbs (1944), may usefully be applied to plumages and molts, and that descriptive and comparative plumage studies will proceed in a more orderly fashion if they are conducted in the light of such a homology concept. It is, of course, impossible to be certain that plumage sequences which appear to be exactly equivalent in various groups of birds are truly homologous in the phylogenetic sense; however, we believe it is not only useful but even necessary to treat such equivalence provisionally as homology in studies of the type we have mentioned.

A few groups of birds present exceptionally difficult problems of interpretation when attempts are made to fit them into the system of homologies here proposed. Further study of some of these difficult groups, which will be mentioned later, may ultimately prove them to be real exceptions to the general pattern, with sequences of plumage succession which have evolved independently. On the other hand, their apparent nonconformity may someday be resolved and their sequence of plumage succession shown to be merely extreme modifications of the general pattern.

Various drafts of the manuscript have been read entirely or in part by many of our colleagues; we are grateful for their comments and helpful suggestions. We wish particularly to acknowledge the constructive criticism given us by Ralph S. Palmer, Thomas R. Howell, Finn Salomonsen, Eugene Eisenmann, and Charles H. Blake.

2. DEFINITIONS

Any description of the plumage succession of a species depends ultimately on the way in which the terms "plumage" and "molt" are defined. Ambiguous use of such words makes it difficult to arrive at straightforward interpretations for any one species, and virtually impossible to trace homologies.

(1) *Cycle.* In most birds of temperate regions, which are the best known, there are several cyclic phenomena which coincide with the

calendar year: reproduction, migration, molting, etc. It is convenient, for such birds, to speak of "number of plumages *per year.*" But there is increasing evidence that some equatorial, antarctic, and oceanic species may have reproductive cycles of less or more than a calendar year, viz., the 9.6-month nesting cycle of Ascension Island Sooty Terns *(Sterna fuscata)* (Chapin, 1954), and the 14- to 18-month breeding cycle of South Georgia King Penguins *(Aptenodytes patagonica)* (Stonehouse, 1956). Although little is yet known on this point, the cycles of plumage succession in such species may also be of more or less than a year. Since our aim in this paper is to suggest homologies of plumages (and a resultant nomenclature) applicable to birds of any part of the world, we will be, for the most part, using the expression "per cycle" rather than "per year." "Cycle" in this sense is to be understood as a shortened version of "plumage cycle;" a "cycle" (in an adult bird) runs from a given plumage or molt to the next occurrence of the same plumage or molt.

(2) *Plumage.* This is much more difficult to define than it would first appear. Dwight (1900) differentiated between "winter" and "nuptial" plumages, even when no molt intervenes, in order to describe those birds which change their appearance markedly through wear. But he even extended this two-plumage concept to birds which do not change their appearance at all (*cf.* the two "plumages" of *Progne subis,* Dwight, 1900: 225). This concept of individually-named plumages attained by either molt *or* wear is probably not widely accepted at present. If followed to its logical conclusion, it would be necessary to state that the adult male Bobolink *(Dolichonyx oryzivorus)* has *three* plumages: the "winter," which is lost by a complete molt, the "spring," and the "summer," attained through wear.

Another type of plumage definition based on the over-all appearance of the bird involves those species in which a molt may be greatly protracted or even temporarily suspended; that is, virtually divided into two stages by a pause in the process of feather replacement. The temptation is then to give separate plumage names based on the appearance of the two stages of the molting bird. As Mrs. Stresemann (1948: 190) puts it, "The resumption of feather growth after a period of interrupted moult does not mean at all that a new plumage is assumed. . . . Many of the Palaearctic migrants, for example, divide their principal moult into two periods. They moult part of their plumage (usually the entire body plumage) before migration, while the remainder of the plumage (usually wing and tail feathers) is not moulted until several weeks later in the winter quarters (as in *Hirundo, Delichon,* and *Riparia*)." This is also true of certain Nearctic migrants, for example many Tyrannidae.

For purposes of homology we feel that it is necessary to confine the word "plumage," as used in studies of plumage succession, to

a single generation of feathers. Such a generation may include less than the entire feather covering of a bird; thus the feathers attained by a partial molt constitute in themselves a plumage by this definition. Perhaps the most important point to stress here is that by our definition the number of plumages is equal to the number of molts in a given cycle. Salomonsen (1941, 1949) described and named no less than four "plumages" for the Oldsquaw *(Clangula),* although admitting that no feather is renewed more than three times per cycle, and most feathers only once or twice. According to our concept, the plumages of the Oldsquaw are homologous with those of other ducks, *except* for the fact that an additional generation of feathers, including only the scapulars and parts of the head, occurs during each cycle. These few feathers constitute the only additional "plumage" of the Oldsquaw, all others being homologous not only with the plumages of other ducks but of other birds in general.

The traditional concept by which a bird can wear only one "plumage" at any given time, the "plumage" being described in terms of the bird's *appearance* rather than of the particular generations of feathers producing this appearance, makes the determination of plumage homologies difficult if not impossible. In birds with greatly protracted molts the appearance may be changing continually, and subdivision into "plumages" on the appearance basis must be, to say the least, arbitrary.

Several authors, including Dwight and Meylan (1932) have used the term "compound plumage." By their definition, a bird wears a "simple plumage" following a complete molt, and a "compound plumage" after a partial molt. By our definition, this is impossible; after a partial molt the bird wears the newly assumed plumage plus parts of one or more previous plumages rather than a single "compound" plumage.

The various semantic difficulties outlined above arise, we feel, out of a real need for additional terms. If a bird at a given time may, according to our usage, be wearing feathers belonging to two or more plumages, how may the bird best be described at that moment? To aid in resolving these difficulties, two additional terms appear to be necessary, as follows:

(3) *Aspect.* This word may be used in descriptions of the total *appearance* of a bird at any given time, no matter how many generations of feathers combine to produce that appearance. Aspect also takes into account changes in appearance brought about by adventitious factors such as fading, staining, and abrasion (wear). In field guides or other simplified descriptions, it will be possible to describe

and portray the "spring aspect" or "winter aspect" of a given species, without reference to plumage names or to actual stage of molt. Thus, a frequently seen late summer aspect of young Starlings *(Sturnus vulgaris)* consists of a grayish-brown head, white-spangled black body, and blackish wings and tail. A given aspect may be analyzed in as much detail as seems desirable.

It is thus apparent that Salomonsen (1941, 1949) has divided various stages of the three plumages of the Oldsquaw into four aspects, which he has designated as "plumages."

(4) *Feather coat.* This term may conveniently be used when it is desirable to describe the aggregate of feathers worn by a bird regardless of the relative time of assumption of the components of that aggregate. The feather coat may, at any given moment, consist of feathers of one, two, or more plumages, i.e., generations of feathers. Descriptions of the feather coat may be made whether or not a molt is under way at the time. Thus, the feather coat of young Starlings during a frequently observed stage of molt in late summer comprises head feathers of the juvenal plumage and body and flight feathers of the next succeeding plumage.

Enumeration of the components of the feather coat actually represents an analysis, in part, of the elements which produce a given aspect (although adventitious factors are irrelevant in describing a feather coat). It should be pointed out that the *aspect* of an individual living bird or specimen can be described even though the plumage sequence of its species is not well enough understood to permit analysis of the components of its *feather coat.*

When, later in the present paper, it is necessary to refer to "plumage" in Dwight's sense (a combination of our concepts of feather coat, aspect, and plumage), the word will be enclosed in quotation marks to distinguish it from the term as we use it in a restricted sense.

A few of our colleagues, on reading this paper in manuscript, have felt that we have given an unduly restricted definition to the word *plumage* by limiting its use in technical discussions of plumage sequence to a single generation of feathers. As has been shown, the word "plumage" as formerly used is a vaguely-defined combination of three different concepts. We feel that it is desirable to continue to use the word *plumage* for one of these three concepts rather than to abandon the word and introduce three new terms; a technical discussion of the molts of a bird without any use at all of the word *plumage* is almost unthinkable. Even though, as used in such expressions as "juvenal plumage", "first winter plumage", etc., in the past, the word "plumage" does not always conform to our restricted definition, we feel that this word carries an established implication of a *stage in a sequence.* It seems logical, therefore, to choose a restricted definition of *plumage* as we have done in order to be able to continue using the word in

technical discussions of the sequential phenomenon of feather replacements. As so used, there can hardly be confusion with the broadly descriptive use of the word *plumage* as in such expressions as "brightly-plumaged birds," "lax plumage," "worn plumage," etc.

(5) *Molt.* A molt may be defined as the normal *shedding of feathers and the replacement of most or all of these by a new generation of feathers.* This definition holds no matter how few feathers are involved and regardless of the time required for this process. The feathers which are shed during a given molt may belong to a single generation or may include feathers, belonging to earlier generations, which have survived one or more previous molts.

The definition of molt given above includes two distinct phenomena: The shedding of feathers and the growth of new feathers. The loss of feathers during normal molting has relatively little physiological impact on the organism. The development of a generation of new feathers, on the other hand, is profoundly interrelated with other physiological processes, affecting some and being affected by others.

Some authors have sought to restrict the term "molt" to the loss alone, using an additional term for the subsequent growth of new feathers. This is an unnecessary and erroneous restriction; the word "molt" is derived from the Latin *mutare,* "change", implying the substitution of the new for the old.

There is evidence (Staebler, 1941) that some birds of northern latitudes have evolved a mechanism whereby more individual body feathers are worn in winter than in summer, presumably by losing feathers from certain follicles in the spring and not replacing these until the autumn. There are several ways in which this adaptation may have developed. Elaboration on this topic would be peripheral to the present paper, but it should be stated that such adaptations can be interpreted within the framework of the concepts here presented.

In birds which renew all their feathers only once per cycle, the process of feather replacement may occur (1) through all or most of the year as a protracted molt, (2) during a relatively brief period at a particular time of year, such as just after nesting, or (3) in several, temporally isolated periods; thus, part of the molt might occur during a brief period in the summer and another part after the bird had reached the wintering ground. In other words, a single molt may be temporally extended or compressed, continuous or discontinuous. In addition, the temporal position of a particular molt may be shifted so that it may commence immediately upon the

completion of the prior molt, or, in certain groups, even before completion of the prior molt. The best known example of such overlapping molts occurs in certain ducks. The molting of the remiges in these ducks has been widely accepted as the last portion of the molt into the "eclipse plumage." Before the growth of the remiges is completed, the next molt is initiated; see description of a specimen of Velvet Scoter *(Melanitta fusca)* in Witherby *et al.* (1943, vol. 3: 355).

We use "partial" and "complete" in their traditional senses; the latter for the assumption of a generation of feathers by the renewal of all tracts, the former for the assumption of a generation involving only specific portions of the bird's covering of feathers. Most adult birds have at least one complete molt per cycle; many have one complete and one partial molt. Some adult birds acquire two different plumages by two complete molts per cycle. Adults of a very small number of species have one complete and two or three partial molts per cycle. Thus, any given feather follicle may be activated once, twice, or rarely three or four times per cycle.

An additional point on usage may be mentioned here. For reasons of clarity, we prefer in general to confine the noun "molt" to the entire change between plumages, and when dealing with an individual feather or group of feathers (but less than an entire generation), to use the present participle, thus: (a) this species undergoes a partial *molt;* (b) the *molting* (not "molt") of the rectrices is centrifugal.

In summary, it may be said

1) A molt consists of the normal shedding of feathers and the replacement of most or all of these by a new generation of feathers, a process which occurs periodically in more or less definite relationship to other events in the life history of an individual bird. This excludes accidental loss and replacement of feathers.

2) Within a single cycle of plumage succession, feathers of various tracts may be renewed once, twice, or (rarely) three or four times.

3) A bird can have no more molts in a single cycle of plumage succession than the maximum number of times any feather follicle is activated.

4) Within a cycle, a molt may be protracted or compressed in time.

5) A molt may be continuous, limited in time, or interrupted in time.

6) The temporal position of a homologous molt in the cycles of plumage succession may vary among different groups of birds or among individuals of a species.

7) A molt may commence immediately upon (or in certain groups even before) completion of the prior molt.

8) The characteristics of a molt may vary with the age, sex, or geographic origin of an individual, and may be influenced by environmental factors.

3. CURRENTLY ACCEPTED CONCEPTS OF PLUMAGE SUCCESSION

Although several authors, including Mayaud, A. H. Miller, Pitelka, Portmann, Salomonsen, Schiøler, Stresemann, Sutton, Witherby, and others, have published papers on specific problems involving molts and plumages, there has been no recent general paper on the subject. Current practices with regard to naming molts and plumages, and the works of Dwight and Meylan, indicate rather clearly the nature of the assumptions underlying currently accepted concepts of plumage succession.

The so-called "nuptial plumage," according to presently accepted views, is common to all "adult" birds, as is the "postnuptial" molt. Plumage equivalences of the sort to which we have applied the homology concept have been established largely in relation to the postnuptial molt. In the words of Dwight (1900: 130): "The only invariable moult is the postnuptial, which, except in a very rare few cases, is absolutely complete and takes place in all species at the close of or soon after the breeding season peculiar to each." Since the postnuptial molt takes its name from the "plumage" preceding it, it is obvious that either the molt or the "plumage" or both may be used as landmarks of homology.

A fundamental assumption, with which we concur, is that most normal adult birds have at least one complete molt per cycle; the molting of any feather which is normally renewed only once per cycle is thus part of this molt no matter when it occurs. This molt (usually called the "post-nuptial" or "complete annual") *and* the "plumage" preceding it have been generally assumed to be equivalent in most birds.

Correlation with the reproductive cycle has also been used in attempting to determine equivalence of plumages, as implied by the last portion of the passage quoted from Dwight, above. Birds with but a single plumage and one molt per year must obviously be wearing their "nuptial plumage" the year round. Many birds have, in one or both sexes, two plumages per year, one of which is a bright "nuptial plumage" usually correlated with reproductive behavior and lost by a complete molt, and the other a dull "non-nuptial plumage" which is partially lost during the partial "prenuptial" molt.

The "reproductive plumages" worn by adult birds, whether they have an additional "non-nuptial plumage" or not, have been con-

sidered equivalent, particularly in view of the fact that these "reproductive plumages" are almost always lost by a complete molt. This relationship constitutes the fundamental basis of what might be called current concepts of plumage homologies. The various so-called "immature plumages" are interpreted by working backwards from the first postnuptial (complete) molt as a landmark and counting the "plumages" (usually two or three) between it and the "natal plumage."

On the basis, then, of current concepts of plumage homologies as outlined above, the plumages of an adult bird with one plumage per cycle (example, the Starling) and an adult bird with two "plumages" per cycle (example, the Scarlet Tanager, *Piranga olivacea*) may be diagrammed as in Figure 1.

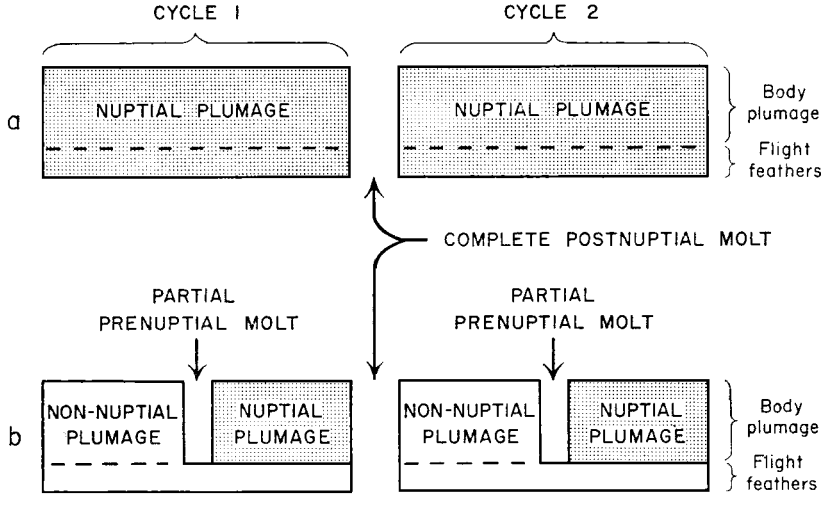

FIGURE 1. Schematic presentation of traditional concept of sequence of molts and plumages in mature individuals of (a) Starling *(Sturnus vulgaris)* and (b) Scarlet Tanager *(Piranga olivacea)*. In these two species one cycle corresponds to one year; two cycles (two years in this case) are illustrated. Stippled areas signify "bright" plumage; white areas signify "dull" plumage. In this and Figures 3–7, molts are shown symbolically; the diagrams merely indicate the sequence of molts and plumages characteristic of each of the species. *The diagrams are not intended to show temporal position or duration of any of the molts, or extent of partial molts.*

4. A NEW APPROACH TO PLUMAGE AND MOLT HOMOLOGIES

There are several weaknesses in the currently accepted concepts outlined in the previous section. One of the most important of these involves the use of the postnuptial molt as the critical landmark of

homology; the "plumages" *preceding* the postnuptial molt of different birds have been considered equivalent. The idea that it is the "nuptial plumage" that is followed by the complete molt in all birds was expressed by Dwight (1902: 249) as follows: "From time immemorial, the adult plumage of the breeding season has been accepted as the one most typical of the species, and the moult by which it is entirely swept away forms a fixed point in every plumage cycle. The plumage may well be called the nuptial and the moult the postnuptial." Thus the criterion for the homology of the "nuptial plumage" is the molt by which the nuptial feathers are *lost*. From the physiological standpoint this appears unjustified. The energy expenditure and other physiological changes connected with growth are significant in relation to the *incoming* feathers and have nothing to do with the feathers that have been shed. Determination of feather color, pattern, and shape occurs during the molt responsible for the *development* of the feather.

It seems illogical to establish the homology of a plumage by means of the molt which is responsible for the *loss* of that plumage and for the development of the *next* succeeding plumage. Yet this is precisely what is done when the postnuptial molt is used as a landmark to identify (as the "nuptial plumage") the "plumage" which *precedes* it.

The idea that the complete molt is homologous in most birds makes more sense if we associate this complete molt with the *incoming* generation of feathers. If we assume the complete molt to be homologous in most birds, then the plumage which *results from* (not precedes) this molt may more properly be deemed homologous in these birds.

Associating the complete molt with the feathers assumed thereby will also clarify the problem of the so-called "compound plumages." In most birds with two "plumages" per cycle, according to Dwight's concept, all feathers (body and remiges) are shed at the complete postnuptial molt and are replaced by a complete set of non-nuptial feathers. A partial prenuptial molt, involving body feathers but not remiges, then renews the "nuptial plumage." Therefore, when the bird is in "nuptial plumage," it is carrying *non-nuptial remiges;* i.e., remiges assumed at the postnuptial molt. However, in a bird with only a single plumage per cycle (which we have seen must, by definition, be the "nuptial plumage" in the traditional sequence), the remiges *must* consist of nuptial feathers and thus *cannot* be equivalent to the remiges of birds with two plumages per cycle. In other words, to use the same two species for illustration, the wing feathers lost by the Starling at its complete molt are nuptial feathers; those lost by

the Scarlet Tanager, having been attained with the "non-nuptial plumage," are non-nuptial feathers, and therefore *not* homologous with those lost by the Starling—*if* the traditional reasoning be pursued down the line.

These discrepancies may be resolved, first, by naming all molts on a "pre-" basis. All feathers which are renewed only once per cycle will then belong to homologous plumages regardless of the number of molts per cycle undergone by other feathers on the bird. Since the plumage attained by the complete molt of different birds is to be considered homologous, it follows that the plumage assumed at this molt by the Starling is homologous not with the "nuptial" but with the "non-nuptial" plumage of the Scarlet Tanager. The "nuptial" plumage of the latter is an "added" plumage assumed by an incomplete molt without counterpart in the Starling.

5. A PROPOSED PRACTICAL TERMINOLOGY OF MOLTS AND PLUMAGES

Of the various early efforts to arrive at a uniformly applicable terminology of molts and plumages, the system proposed by Dwight (1900, 1902, 1905) has been the foundation of most, if not all, subsequent work. Palmer (1955) and others have modified Dwight's original terminology in an effort to achieve a more truly universal applicability. Some authors (notably Salomonsen, 1939, 1941, 1949) who have studied intensively the molts of groups of birds presenting special difficulties of interpretation (e.g., *Lagopus, Clangula*) have found Dwight's terminology misleading or inadequate and have, for descriptive purposes, erected a special terminology for their subject species. The terminology has been further complicated by use of the same word "plumage" for the concepts for which we employ the separate terms "plumage," "aspect," and "feather coat."

All proposed systems of nomenclature for molts and plumages known to us have in common the fault that they derive all or part of their terminology from seasonal, reproductive, developmental, or other phenomena. Ideally, the plumage cycle should have an *independent* terminology so that molts and plumages may be considered *in relation to* other cyclic phenomena rather than named *in terms of* such phenomena. Such an independent terminology will permit clear expression of the differences in the relationship of plumage cycles to other cycles among various birds.

Dwight's original nomenclature (1900) was based partly on the seasons ("winter plumage") and partly on the reproductive cycle ("nuptial plumage"). There are obvious disadvantages to naming a plumage sequence by reference to seasons. Homologous plumages

may be worn by different birds at different seasons, even within a single species. Northern Hemisphere migrants are wearing their "winter plumage" in the Southern Hemisphere during the local summer. The terms are quite meaningless in the equatorial regions where many cyclic phenomena are correlated with dry and rainy periods rather than "summer" and "winter" (*cf.* A. H. Miller, 1954). We have already mentioned the likelihood that the plumage cycles of some birds may be less or more than a calendar year. This is also a reason to abandon the widely used term "annual molt."

Another difficulty with seasonal terms involves the relationship of plumage-names and molt-names. The nomenclature should, in some way, relate the molts and the plumages, but this has not usually been done when seasonal terms were used. When similar names *are* used for both plumages and molts, e.g., "summer plumage," "summer molt," it becomes necessary for the author to explain carefully whether (a) the molt is being named *in relation to the plumage* or merely on the basis of *season of actual molt,* and (b) if the former, whether the "summer molt" is that by which the "summer plumage" is *acquired* or *lost.*

Dwight (1902), Palmer (1955), and others, having eliminated these undesirable seasonal terms, rely principally on terms relating the plumage cycle to the reproductive cycle. Thus the plumages are called nuptial and non-nuptial, breeding and non-breeding, nesting and non-nesting, etc. Such terminologies are more nearly universally applicable than are the seasonal type, and have thus had wide acceptance. However, terminologies dependent on stages of the reproductive cycle have important undesirable features of their own. The relatively little that is known about the actual relationships between these two physiological cycles in most birds indicates that these relationships are highly variable (see, for example, Wolfson, 1954; Marshall and Disney, 1957; Miller, 1954). It therefore appears unjustified to link them in a fixed system of nomenclature. Relationships may better be defined and studied if the terminology carries no preconceived implications of dependency.

In addition, the use of plumage names based on the reproductive cycle results in misnomers when applied to the many species of birds which do not breed until after their first year. If followed unswervingly, such a terminology results in such awkward and self-contradictory circumlocutions as "1st Nuptial (Non-Breeding) plumage" (Palmer, 1955). In this same connection, a truly uniform terminology should make allowances for a species which may carry on its courtship displays in a plumage *not* homologous with the so-

called "nuptial" plumage of most birds. Salomonsen (1939: 397) points out that the display of the male Rock Ptarmigan *(Lagopus mutus)* "takes place in full S[ummer]-plumage in Scotland, in a particoloured, partimoulted dress in Scandinavia and in the pure white W[inter]-dress in Northeast Greenland." Obviously in this species no one plumage may correctly be called a "nuptial" plumage in the functional sense.

Perhaps in an effort to avoid some of the pitfalls listed above, some authors have resorted to purely descriptive names for plumages, such as bright vs. dull, ornate vs. plain, etc. The one descriptive term which has found widespread acceptance is "eclipse"; although used almost universally for ducks, it has also been applied to the "dull" or "winter" plumage of other groups, particularly the sunbirds (Nectariniidae). The word "eclipse" implies a dull plumage worn for a short time by an otherwise brightly colored bird, such as the male Mallard *(Anas platyrhynchos.)* The word becomes meaningless when an attempt is made to apply it to birds in which *both* stages of the plumage cycle are dull in color, such as the female Mallard or both sexes of the Black Duck *(Anas rubripes).* Further, the "dull" plumage assumed by males of the brightly colored ducks at an age of 12 or 14 months is universally called the "first eclipse" in spite of the fact that many (perhaps most) ducks have a homologous plumage immediately succeeding the juvenal plumage; the so-called "first eclipse" is therefore actually the *second* eclipse when viewed in the light of developmental homology!

Some authors, for example Witherby *et al.* (1943-1944), have partially circumvented the terminology problem by using definite names for certain plumages only, particularly those of young birds; nestling, juvenile, etc. For adults, the aspect rather than the plumage is described. This procedure is of use principally from the viewpoint of the field observer and is of little value in a detailed discussion of molt and plumage cycles in various groups of birds.

The terms used by Witherby *et al.* for the plumages of young birds (see above) introduce the problems of a terminology based on age, or developmental stage of the bird. Rather than naming the plumage itself, this method actually describes the *age of the bird* which happens to be wearing a particular plumage. Such a terminology concerns itself with such chronological events as the young bird's attainment of independence of its parents, or flight, or sexual maturity—that is, whether or not the bird breeds or is able to breed in the particular plumage. In practice, regardless of what terminology is used, it is always desirable to state chronological age at which a plumage or molt

occurs, a bird first breeds, etc. A hybrid terminology, combining developmental and plumage-stage characteristics, was proposed for use by bird-banders (Michener and Farner, 1948).

Some of the objections to an age-based terminology are similar to those cited above in connection with plumage names based on the breeding cycle. There are enough cases of species known to court or actually breed in plumages other than the so-called "adult" for the disadvantages of naming plumages in terms of supposed sexual maturity to be obvious. An ideal nomenclature would not permit us to speak of sexually mature birds breeding in "subadult" or "immature" plumages, as we so often do now. Different species obviously may be wearing different plumages (from the developmental standpoint) when they first become sexually mature.

It is thus our contention that currently used terminologies for molts and plumages have a sufficient number of serious drawbacks to warrant a thorough revision. We have no argument with the findings of modern workers regarding the nature and pattern of plumage succession of birds as it may be related to seasonal rhythms, reproductive cycle, ontogeny, and various other environmental and endocrinal phenomena. We do contend, however, that these phenomena may be related in different ways in different groups of birds, and that these relationships can only be obscured by making the nomenclature of plumages and molts contingent on stages of any other cycle or developmental process. There is clearly a need for a semantically "clean," independent, uniform, and practical terminology applicable to plumages and molts of all birds. The desirable attributes of such a terminology may be listed as follows:

1) The nomenclature must consist of terms which are independent of other terminologies applied to birds.

2) It must be capable of expressing homologies, and therefore must be based on some reasonable assumptions upon which to fix the homologies.

3) The nomenclature must be flexible; i.e., adaptable to all known (and reasonable, yet so far undiscovered) modifications of the patterns of plumage succession.

4) The nomenclature must be consistent and as simple as possible.

We are fully aware of the vast amount of work yet to be done, particularly on the more aberrant groups of birds, before anything like a full understanding of the biology of molts and plumages can be achieved. Our aim is to present what we believe to be an improved means of communication for presenting the results of such studies.

We endeavor also to introduce a terminology of molts and plumages which will assist in clarifying homologies.

We advocate retention of the familiar term juvenal plumage for the first covering of true feathers. As mentioned in the introduction, the juvenal plumage itself does not come within the scope of the present paper, but is mentioned here because we begin with the replacement of the juvenal feathers. This has traditionally been known as the "postjuvenal molt," and described as either "complete" or "incomplete" by Dwight and other authors. However, since *all* of the juvenal feathers are eventually lost and replaced, it is misleading to speak of an "incomplete postjuvenal molt." Since several molts may be involved in the replacement of all of the juvenal feathers, the collective term "postjuvenal feather replacement" may be used when this phase of plumage succession is being studied, but it should *not* be used as a formal molt name. As mentioned earlier, we believe that molts should be named in terms of the incoming generation of feathers; thus, instead of "postjuvenal molt," we conceive of the total postjuvenal feather replacement as being accomplished in one or more "pre-" molts.

In birds which have, as "adults," one plumage per cycle (*viz.* the Starling), this plumage is almost invariably lost and renewed by a complete molt. We have selected the term **basic** for this plumage. The molt by which the basic plumage of "adults" is renewed is thus the *prebasic molt.* Although complete in "adults," this molt may be either complete or partial in young birds undergoing postjuvenal feather replacement.

In birds which have, as "adults," two plumages per cycle (*viz.* Scarlet Tanager), the complete molt is again the prebasic molt, followed by the basic plumage. The basic plumage in such birds is followed by another plumage, i.e., generation of feathers (usually comprising feathers other than the remiges and rectrices), which we propose to call the **alternate** plumage. The intervening molt is thus the *prealternate molt,* usually partial, but complete in some species (viz. the Bobolink). In most birds with two plumages per cycle, the basic plumage is completely renewed every cycle, while for part of the cycle the feather coat is a composite of retained basic feathers (usually remiges and rectrices) plus body feathers of alternate plumage attained at the partial prealternate molt.

A few species have evolved a cycle in which, as "adults," more than two molts occur. The plumage resulting from such an additional or supplementary molt is called the **supplemental** plumage.

Such a plumage may be inserted in the typical two-plumage cycle either before or after the alternate plumage; its position will depend on the functional basis for the evolution of such an additional plumage. Much additional work is needed on the plumage homologies of those species in which a supplemental plumage has developed.

For those species (such as the Herring Gull, *Larus argentatus*) in which age classes are identifiable for the first year or more through plumage characteristics, the names of the plumage stages may bear numerical prefixes such as first prebasic molt, first basic plumage, first prealternate molt, etc., as needed. Traditionally, the plumage which, once attained, does not change further with age has been called "adult;" thus, "adult nuptial plumage," "adult non-nuptial plumage," etc. But, as mentioned earlier, the word adult when used in this connection, has an implication of sexual maturity which is misleading, since many species of birds may breed before attaining "adult" plumages. Therefore, we suggest the term **definitive** for those plumages which do not change further with age; thus it might be said of a given species that its second alternate plumage is followed by its definitive basic plumage. All plumages may not reach the definitive condition during the same year of a bird's life; thus, the often bright and ornamental alternate plumage may not reach the definitive condition in some birds until the third or fourth year, while the more conservative basic plumage may not undergo any further detectable change after the second year.

After the juvenal plumage has been lost, the plumages of a bird are ordinarily acquired and lost in cyclical fashion. For example, the male Scarlet Tanager, a bird with two plumages per cycle, and first-year individuals recognizable as such, has a cycle which may be diagrammed as in Figure 2.

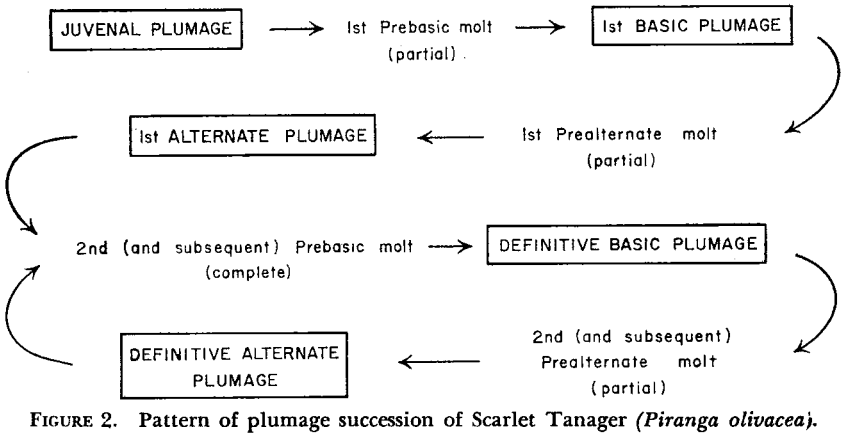

FIGURE 2. Pattern of plumage succession of Scarlet Tanager *(Piranga olivacea)*.

To clarify further our interpretation of the homologies of molts and plumages, we present below a comparative list of our proposed nomenclature (which reflects our interpretation of homologies) and the nomenclature of Palmer (1955), which is modified from that of Dwight (1902). The list shows the nomenclature for a bird with two plumages per cycle; the names of those molts and plumages missing in birds with but a single plumage per cycle are enclosed in square brackets []. The few special cases involving supplemental plumages are not shown here. Plumage names are in **bold face,** molt names in *italics.* It should be noted that the starred (*) terms in the left-hand column are usually not plumages as we have defined the word, but are in most cases applied to feather coats consisting of more than one plumage.

OLD	NEW
juvenal	**juvenal**
postjuvenal	*first prebasic*
*[**first non-nuptial**]	**first basic**
[*first prenuptial*]	[*first prealternate*]
***first nuptial**	[**first alternate**]
first postnuptial	*second prebasic*
[**second non-nuptial**]	**second basic**
[*second prenuptial*]	[*second prealternate*]
***second nuptial**	[**second alternate**]
etc.	etc.

The old and new concepts of plumage homology and nomenclature are compared diagrammatically in Figure 3.

We are well aware that difficulties will be encountered in applying this terminology to certain groups of birds. In some cases this will prove to be due to incomplete knowledge of the molts and plumages of that group, and further study will show that such birds conform to the pattern of homology outlined above, with, of course, their own specialized modifications of the pattern. Other cases may well show that parts of our fundamental thesis need to be altered or broadened. We feel, however, that an understanding of the most prevalent patterns of plumage and molt and their homologies is a necessary prerequisite to the study of groups which may seem to depart from those patterns, and we believe the system outlined above will aid materially in gaining such an understanding. Examples of the problems which will eventually need to be studied from the viewpoint of homology may be found among the loons *(Gavia),* the leaf-warblers *(Phylloscopus),* and the sunbirds *(Nectariniidae).*

There is much controversy and confusion in the literature with respect to the wing-molt of loons; the remiges have been stated to be shed (1) at the prebasic molt in the fall; (2) at the prealternate molt in the spring (thus making the prebasic molt partial and the prealternate complete, a reversal of the normal

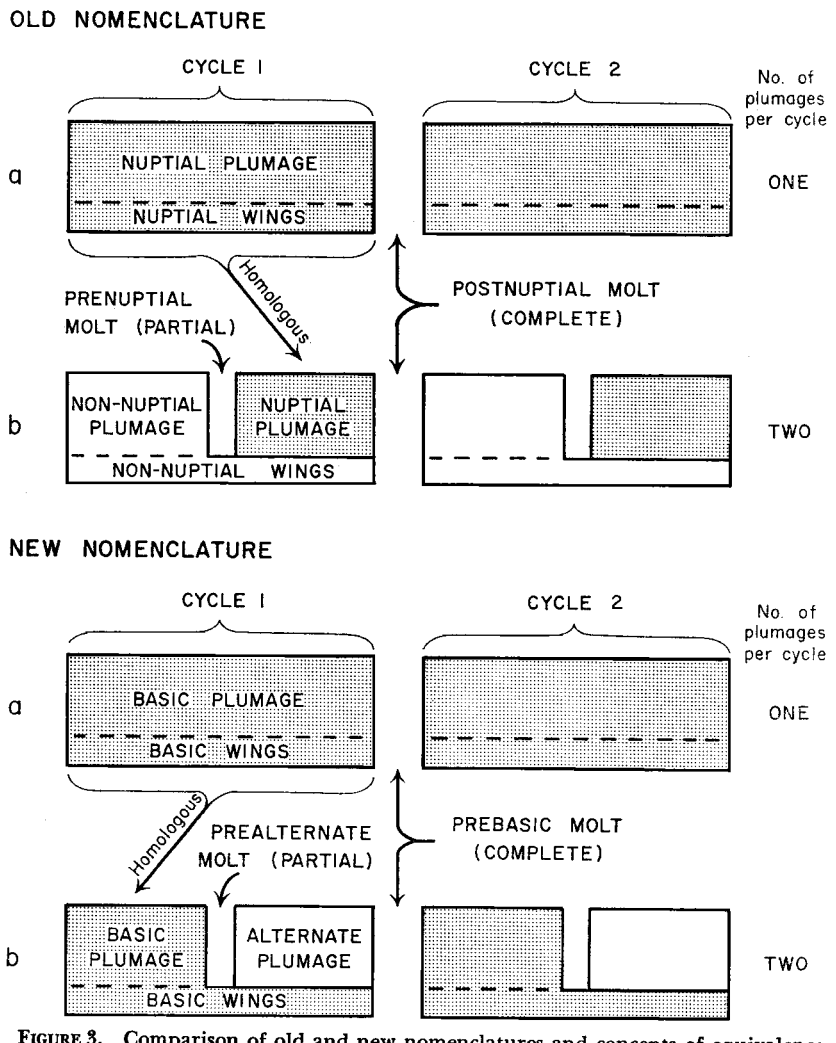

FIGURE 3. Comparison of old and new nomenclatures and concepts of equivalence. Stippled plumages are considered equivalent in each case.

situation); or (3) twice, both in spring and fall. There may be variation of the wing-molt within the genus *Gavia* or even within a single species.

In *Phylloscopus* there appears to be an unusual amount of variation in the extent of the molt or molts. Among the species described by Witherby *et al.* (1943, vol. 2: 1–27), the following patterns of feather replacement are listed: complete prebasic, no prealternate *(P. schwarzi);* complete prebasic, partial prealternate *(P. collybita, inornatus, proregulus, fuscatus); partial* prebasic, *complete* prealternate *(P. trochiloides, sibilatrix, borealis);* complete prebasic, complete prealternate *(P. trochilus).* A detailed study of molt patterns in *Phylloscopus*

would obviously be rewarding, since at least three species are said to reverse the normal pattern of complete prebasic and partial prealternate molts.

It is possible that in certain species of sunbirds *(Nectariniidae)* the dull basic plumage may be completely suppressed, since males of some species molt directly from a bright to a bright plumage, while in other, closely related species, the males wear a dull "eclipse" plumage for part of the cycle (Mackworth-Praed and Grant, 1945). The matter is further complicated by the variation among closely related species in presence or absence of a dull plumage between the juvenal and first bright plumages. This family thus presents one of the most challenging problems in the study of plumage succession. The theory that the basic plumage may have been completely suppressed in some sunbirds is buttressed by the situation in many ducks, in which the first basic plumage is rudimentary (Schiøler, 1921 and 1925), and the later basic plumages are held for but a few weeks and may even be partly or completely lost in some individual birds (Hochbaum, 1944: 112). As emphasized above, the more thoroughly the typical patterns are understood, the more conspicuous will be these and other apparent exceptions which need further study.

6. PATTERNS OF POSTJUVENAL FEATHER REPLACEMENT

As mentioned earlier, postjuvenal feather replacement is invariably complete in the sense that all juvenal feathers are eventually replaced during the course of one (the so-called "postjuvenal") or more molts. There are many variations in the program of postjuvenal feather replacement. Such variations involve not only the number of molts undergone in total replacement of the juvenal feathers, but also the *extent, temporal position,* and *duration* of the molt or molts.

The following variations may occur in the number of molts taking place before postjuvenal feather replacement is completed:

1. One molt, the *first prebasic* (see Figure 4a). Williamson's (1956) study of plumage succession in Anna's Hummingbird *(Calypte anna)* illustrates the occurrence of complete postjuvenal feather replacement in a single prebasic molt. Compare our figures 4a and 8.

2. Two molts, the *first and second prebasics* (see Figure 4b). Steller's Jays *(Cyanocitta stelleri)* completely replace all juvenal feathers in two molts, the first and second prebasic molts, as Pitelka's (1958) excellent study shows. Compare Figures 4b and 9.

3. Three molts, the first *prebasic, first prealternate,* and *second prebasic* (see Figures 4c and 4d). In most species known to us in which three molts occur before the juvenal plumage is completely replaced, *only two* of these molts (the first and second prebasic molts) actually involve shedding and replacement of juvenal feathers. The first prealternate molt in these species replaces first basic feathers—*not* juvenal feathers. This pattern of postjuvenal feather replacement is described by Miller (1928 and 1931) for the Loggerhead Shrike *(Lanius ludovicianus;* see Figures 4c and 10).

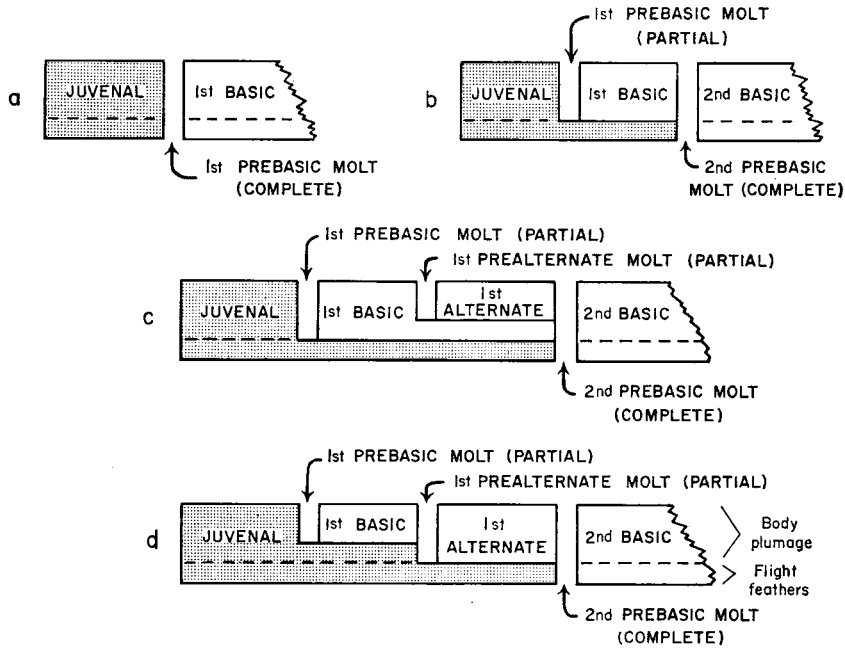

FIGURE 4. Four patterns of postjuvenal feather replacement. The molts are indicated symbolically; no indication has been made of their extent (other than partial or complete), temporal position, or duration. The juvenal plumage may be lost in one molt (a), two molts (b and c), or three molts (d). Stippled areas signify juvenal plumage.

Phillips (1951) has shown that in the Rufous-winged Sparrow *(Aimophila carpalis)* certain of the juvenal wing and tail feathers are replaced at the first prealternate molt. Thus, in at least this one species, some juvenal feathers are replaced in each of three successive molts.

7. PATTERNS OF SUCCESSION OF DEFINITIVE PLUMAGES

One molt and one plumage per cycle.—In this and the following discussions of patterns of plumage succession we will be dealing only with plumage and molt cycles occurring after plumages have become definitive. It is not practicable for us to treat here all of the tremendous number of patterns of plumage succession which occur in nature as a result of combinations of variations in pattern of *juvenal feather replacement, replacement of undefinitive plumages,* and *replacement of definitive plumages.*

Birds with one molt (prebasic) and one plumage (basic) per cycle may or may not exhibit sexual dimorphism of plumage color. The

complete prebasic molt may vary in temporal position, duration, and in order within the molt. The complete cycle may be less than a year (this needs documentation), more commonly a year, or in some cases (some cranes? *cf.* Mayaud, 1950) greater than a year in length.

There are three common variations in "brightness" or "dullness" of the basic plumage in the two sexes. Males and females of many birds (e.g. *Thryothorus, Troglodytes*) wear dull basic plumages (one useful but not invariable criterion of the "dullness" of a basic plumage is general similarity to the juvenal plumage). In an Icterid, the Red-winged Blackbird *(Agelaius phoeniceus),* and many harriers *(Circus)* the male wears a bright definitive basic plumage and the female a dull one rather like that of the juvenal. In some species, such as the Emperor Goose *(Anser canagica)* and the European Robin *(Erithacus rubecula),* both sexes wear a bright basic plumage quite different in appearance from that of the juvenile.

It is clear that "dullness" and "brightness" are more or less subjective terms when used to describe the appearance of a bird's plumage. Also, the appearance of the juvenal plumage may be affected by a wide variety of selective agencies and hence cannot be used comparatively as an invariably trustworthy criterion of the "dullness" of a definitive plumage. The important thing we wish to stress here is that sexual dimorphism of plumage color has developed in various groups of birds having only one plumage and one molt per cycle.

Male with two molts and plumages per cycle, female with one.—Witschi (1935, 1936) states that males of certain weaverbirds *(Pyromelana, Euplectes, Quelea)* have two plumages and molts per cycle, while the females have but one. This needs more study.

The occurrence of a "bright" alternate plumage in males of a species in which the females are alleged to have only a single molt per cycle, wearing the dull basic plumage throughout, is of particular interest since it further supports our contention that the alternate plumage is an "added" plumage. It also supplies us with a condition intermediate between 1) that in which both sexes wear only a basic plumage throughout the cycle, and 2) that in which both sexes have an added alternate plumage as well. This suggests that there are at least two evolutionary paths by which sexual dimorphism of plumage pattern and coloration may be attained: 1) by the *"brightening"* of the basic plumage in one sex, or 2) by the *addition* of a "bright" alternate plumage in one sex.

One complete and one partial molt per cycle in both sexes.—A great many species of birds have two molts per cycle, one complete (the

prebasic) and one partial (the prealternate). Numerous different variations in this pattern of plumage succession are possible. The complete prebasic molt varies in temporal position and duration; the partial prealternate molt varies in extent as well as in temporal position and duration.

The partial prealternate molt may involve only a very few feathers (e.g. *Lanius ludovicianus;* Miller, 1928) or nearly all of the feathers on a bird. The definition of a partial molt might include both the replacement of a single feather and the replacement of all but a single feather. It is impracticable to try to make use of such a refined definition. In most cases partial molts involve the body feathers. If

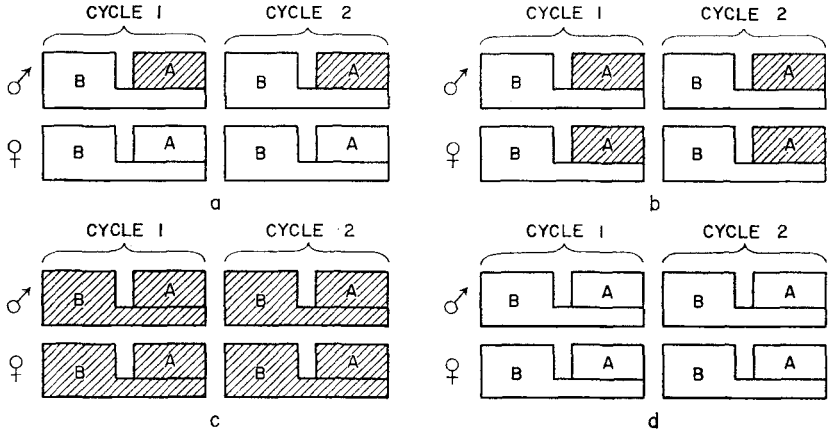

FIGURE 5. Variations in "brightness" and "dullness" of plumage in birds which have two plumages and two molts (one of them partial) per cycle. Shaded areas indicate "bright" plumage; unshaded areas indicate "dull" plumage. B = basic; A = alternate.

any feathers at all are retained, some of the remiges usually are among them. A partial molt will seldom involve *all* of the remiges but *not* the feathers from some other tracts.

Alternate plumages of many birds are sexually dimorphic (e.g. many Anatinae). In species with a sexually dimorphic alternate plumage, the females may change relatively little in aspect at the prealternate molt (e.g. *Anas platyrhynchos*). In other cases, the female, although decidedly "duller" than the male in alternate plumage, is nonetheless "brighter" than is either sex in the basic plumage (e.g., some species of *Dendroica*). The latter situation prevails in the Phalaropes (Phalaropodidae), except that in this family the female is the "bright" sex.

A great many species of birds exhibit seasonal dimorphism in that

they have a non-sexually dimorphic alternate plumage which differs more or less strikingly from the basic plumage (e.g., Podicipedidae, Alcidae, etc.) (see Figure 5b). Such specialized, non-sexually dimorphic alternate plumages presumably have some importance in relation to the reproductive cycle, serving perhaps in mutual displays, or to facilitate species recognition, or perhaps as a response to differing environmental conditions on summering and wintering areas.

The alternate and basic plumages in both sexes are "dull" and practically identical in many species of birds. In some cases (e.g., some waterfowl) this suggests secondary loss of sexual dimorphism of plumage coloration without loss of the "added" alternate plumage. At some time in the history of such species the male alternate plumage was presumably bright in contrast to the dull alternate plumage of the female. This appears to be illustrated well by the Mallard and its insular relatives, *A. wyvilliana* and *A. laysanensis.*

Abrasion of the plumage may have been the selective influence in some species (e.g., Savannah Sparrow, *Passerculus sandwichensis*) bringing about the evolution of an alternate plumage to replace badly worn basic feathers. In such cases the alternate plumage appears to be practically identical with the basic plumage (Figures 5c and 5d).

Two complete molts per cycle.—Very few species are known to have two complete molts per cycle. One such species is the Sharp-tailed Sparrow *(Ammospiza caudacuta),* which shows little sexual or seasonal dimorphism. In the Bobolink, which also has two complete molts per cycle, the male wears a bright alternate plumage which is replaced by a basic plumage like that of the female. The basic and alternate plumages of the female are practically identical.

There may be species in which the male has two complete molts per cycle and the female either 1) only one complete molt per cycle, or 2) a complete and a partial molt per cycle. We are not aware of such species, but this is a possible intermediate stage in the evolution of patterns of plumage succession.

Supplemental plumages.—A few species of birds have three molts and plumages per cycle, the third or supplemental plumage being an "added", usually specialized, plumage in addition to the basic and alternate plumages. Males of the Ruff *(Philomachus pugnax)* have a supplemental plumage, according to Kozlova (1957), while females do not. The Oldsquaw has a supplemental plumage (*cf.* Salomonsen, 1941 and 1949; Stresemann, 1948; and Sutton, 1932). Males and females of three of the four species of ptarmigan have supplemental plumages (*cf.* Salomonsen, 1939). Salomonsen (pers.

comm.) says that Johnsen (1929) has shown that some populations of Willow Grouse *(Lagopus lagopus)* have four generations per cycle of certain feathers. This is the only species, thus far, to which *two* supplemental plumages have been attributed; these may be distinguished nomenclatorially by the letters "A" and "B".

For illustrations showing possible patterns of plumage succession involving three molts and plumages, see Figure 6.

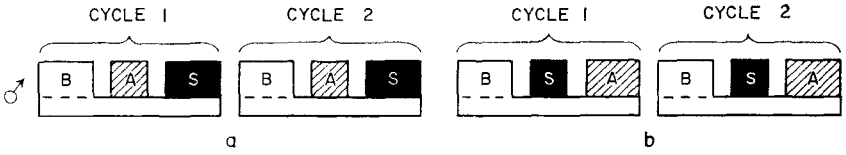

FIGURE 6. Possible patterns of plumage succession in which some feathers are replaced three times during a cycle. Shaded areas indicate alternate plumage; black areas indicate supplemental plumage; white areas indicate basic plumage.

Summary of patterns of plumage succession.—The various patterns of succession of plumages may be outlined as follows:

I. *One complete molt and one plumage per cycle.*
II. *Two molts and two plumages per cycle.*
  A. Prealternate molt partial
  B. Prealternate molt complete
III. *Three molts and three plumages per cycle.*
  A. Presupplemental molt follows basic plumage
  B. Presupplemental molt follows alternate plumage.

Upon these patterns of plumage succession may be superimposed the several variations in postjuvenal feather replacement and in sexual and/or seasonal dimorphism described earlier.

Phylogeny of "bright" plumages.—We believe that the plumages of most birds probably were not originally sexually, seasonally, or developmentally dimorphic (or polymorphic) but were dull or subdued in color and pattern; these "primitive" or "ancestral" plumages were most likely renewed periodically and completely by *protracted* molts.

These assumptions seem to us reasonable because: 1) Dull juvenal and female-like plumages of many sexually dimorphic groups are taxonomically conservative in contrast to the bright sexual plumages of males (Trochilidae, Anatidae, etc.). 2) In sexually dimorphic birds with an "added" sexual (alternate) plumage in males, the nonsexual (basic) plumage in most cases resembles the female and juvenal plumages. 3) The bright male sexual (alternate) plumage of two-

plumaged, sexually dimorphic species, is undoubtedly an "added" plumage since it is acquired (with rare exceptions) by a partial molt, and is present as a "special" second plumage in males of some groups of birds in which females are said to have but a single, dull plumage per year (some Ploceidae). 4) In some groups of birds (viz. Anatidae), some members of which have two molts per year and a bright sexual plumage in males (Anatinae), the species which are considered "primitive" (Anserinae) have but one molt and one plumage per year. 5) Since the plumage comprises approximately ten per cent of the total weight of a bird, replacement of the plumage requires a considerable expenditure of energy. It seems reasonable

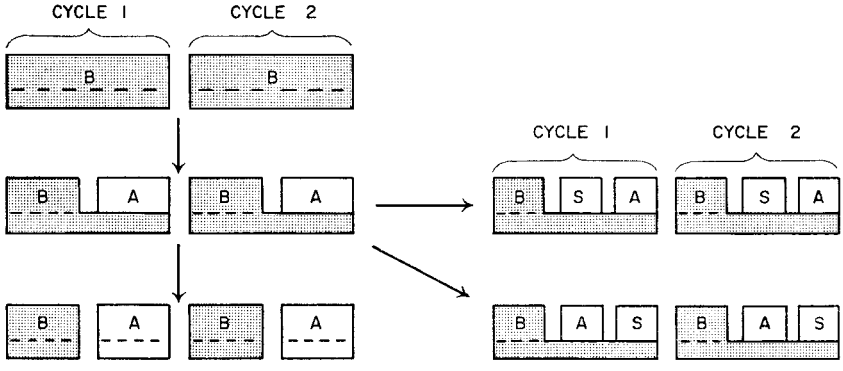

FIGURE 7. Comparison of patterns of plumage succession indicating ways in which increase in complexity may have occurred. Stippled areas indicate basic plumage.

to suppose that primitively this energy expense was budgeted over a fairly long period of time. In view of the total expenditure of energy required for the development of a whole new generation of feathers, temporal compression of molt would be disadvantageous unless counterbalanced by other requirements (*cf.* Lesher and Kendeigh, 1941). Such activities as migration, reproduction, temperature regulation, or development may make it necessary that many feathers be replaced in a short period of time (wing molting in ducks, etc.).

The great existing variability of feather morphology, color, and pattern, and of timing and duration of molts, indicates the presence of many types of selective pressure. It seems reasonable to us to assume that such selection may account for most of the presently known deviations from the generalized "ancestral" or "primitive" condition hypothesized above.

We have not attempted to outline all possible variations in pattern

of plumage succession and their possible derivations; there is too little information for this sort of speculation. However, remembering that the number of molts per cycle and the extent of each may have resulted from any number of selective influences, it is possible to construct a simple diagram which illustrates the several general patterns of succession of definitive plumages, and suggests ways by which these might have been derived (see Figure 7).

8. EXAMPLES

To illustrate in detail the application of our terminology to the three major patterns of postjuvenal feather replacement and the two most common molt sequences, we have selected three species, the molts and plumages of which have been thoroughly described in recent papers. In each of the following discussions, and in the accompanying diagrams, we have paid particular attention to *extent, temporal position,* and *duration* of molts; diagrams of molt sequence prior to Figures 8, 9, and 10, have not taken these factors into consideration and have illustrated molts symbolically without relation to time or extent.

In Figures 8, 9, and 10, the period during which the juvenal plumage is worn is stippled, the period of basic plumage white, and the period of alternate plumage shaded. The black areas represent periods of molt. Variation within the species in the onset and completion of a molt is indicated by the spread along the horizontal axis of the black area (except in Figure 10, for which this information is not available). The duration of molt for a single individual is approximated by the diagonals forming the lateral borders of the black areas. Thus, in Anna's Hummingbird (see Figure 8), the onset of the first prebasic molt may occur at any time from late May to mid-September. An individual which began this molt in late May would complete it early in October.

The diagrams have been divided horizontally by a dashed line to show separately the molting periods of body plumage and flight feathers. Further refinement of the diagrams could be achieved, if desired, by separate plotting of any given feather tract, if sufficient information were available. Thus, for some species it would be desirable to divide the diagram into three parts rather than two, breaking "flight feathers" into remiges and rectrices.

Molts and plumages of the male Anna's Hummingbird.—Williamson (1956) has described the molts and plumages of Anna's Hummingbird in sufficient detail to allow a diagrammatic presentation of the molts of that species (see Figure 8).

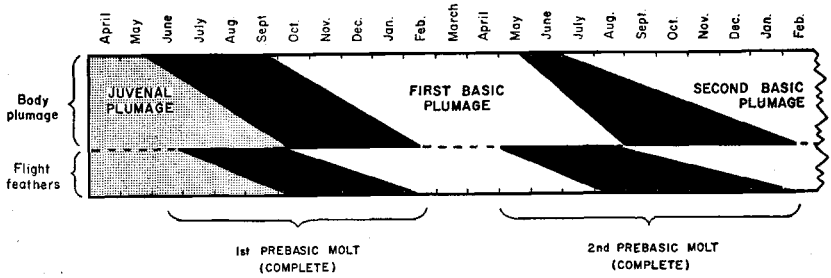

FIGURE 8. Plumage succession in Anna's Hummingbird *(Calypte anna).* See text for discussion. Compare with Figure 4a.

All postjuvenal feather replacement in Anna's Hummingbird occurs during the complete first prebasic molt. This "molt may begin as early as late May, and birds in the earliest stage of molt may be found as late as September. Molt in some birds continues into January and as some of these birds are in a middle or late-middle stage of molt, feather replacement undoubtedly occurs in some instances into February. Thus, on a population basis, molt occurs over a period of eight to nine months. . . . The postjuvenal molt [= first prebasic molt] in the individual is estimated to take approximately four and one-half months. In certain individuals there may be a retardation of molt in winter to the extent that it may require about six months" (Williamson, 1956: 346). "Such retardation . . . may be related to changes in food, qualitative or quantitative, in the course of the fall and early winter. It has been observed in the field that the birds congregate at this time about favorable food sources and the juvenal males are less successful than adults in maintaining feeding territories" (*op. cit.*: 355).

Second and subsequent prebasic molts are complete and take place as follows: "molt may begin as early as the first week in June and . . . even earlier. Refeathering of the head, the last stage in the molt, may occur as late as January. The period of time over which molt may be underway in at least some members of the population is eight months. . . . The total period of molt in the individual is three to three and one-half months." (*op. cit.*: 351).

"The molt of adults is similar in most respects to that of the juveniles. The molt of adults is briefer. . . . It commences in the alar tract, whereas in the juvenile it commences in the ventral tract" (*op. cit.*: 355).

Molt in Steller's Jay.—The molts of a population of Steller's Jay from Graham Island (northernmost of the Queen Charlotte Islands, British Columbia) have been studied in great detail by Pitelka (1958). Figure 9 is based entirely on data drawn from Pitelka's excellent study.

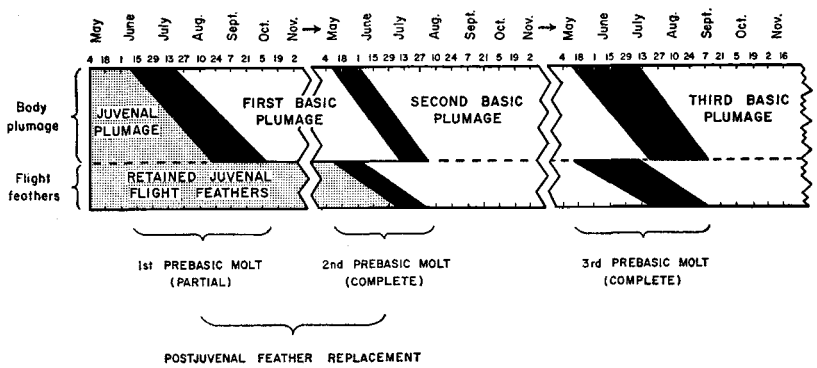

FIGURE 9. Plumage succession in Steller's Jay *(Cyanocitta stelleri)*. See text for discussion. Compare with Figure 4b.

Postjuvenal feather replacement in Steller's Jay is completed in two molts, e.g., the partial first prebasic molt and the complete second prebasic molt. Thereafter, Steller's Jays wear basic plumage and replace it once a year during a complete prebasic molt.

The first prebasic molt "begins in the interval from June 10 to July 20, and juveniles individually take 70 to 80 days to molt" (Pitelka, 1958: 49). "The flight

feathers, alula, greater primary coverts, and a variable number of the greater secondary coverts are retained" (*op. cit.*: 40). The onset of the first prebasic molt occurs shortly before the juvenal rectrices have completed their growth. In Steller's Jays from "lower latitudes there is typically a time gap between the end of growth of juvenal rectrices and the onset of the postjuvenal [= first prebasic] molt" (*op. cit.*: 41).

The second prebasic molt [= Pitelka's "first complete molt"] begins in the interval from May 9 to June 4. Pitelka (*op. cit.*: 42) had insufficient material to determine the ending of this molt or its duration in an individual; he states that "the period of molt in the individual" is "presumably [the] same as other complete molts."

The third and subsequent prebasic molts begin "in the interval from May 12 to July 10, and adults individually take 60 to 70 days to molt" (*op. cit.*: 49). The flight feathers are replaced during approximately the same period as the body plumage.

Molts of the Loggerhead Shrike.—Post-juvenal feather replacement occurs during the first and second prebasic molts in the Loggerhead Shrike; the first prealternate molt as far as known replaces only first basic feathers. The plumage sequence of adults involves two molts: a complete prebasic and a partial prealternate molt.

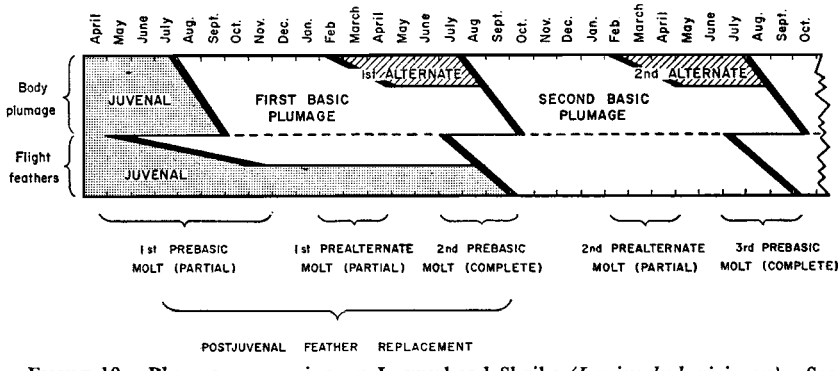

FIGURE 10. Plumage succession on Loggerhead Shrike (*Lanius ludovicianus*). See text for discussion. Compare with Figures 4c and 5b.

A. H. Miller's (1928 and 1931) studies of plumage succession in shrikes illustrate the extensive individual and regional variation that may occur in extent, temporal position, and duration of molt. Figure 10 is a diagrammatic presentation of the sequence of molts in one race (*gambeli*) of the Loggerhead Shrike based on Miller's data. We have not indicated the possible variations in extent, temporal position, or duration of molt. Nor have we attempted to do more than indicate that in the population a given molt occurs during a given period of time.

The first prebasic molt is a partial molt which shows considerable variation in extent. In *gambeli*, approximately 30 to 40 per cent of the population does not renew any juvenal primaries during the first prebasic molt; 95 to 100 per cent of the population replaces all greater secondary upper coverts; and between 70 and 90 per cent of the population replaces all rectrices (Miller, 1931: 133–139). "The time occupied in molting is between three and four months for any

one individual, usually three and one-half months. For a population taken as a whole the total length of the period in which molt may be encountered depends on the length of the breeding season and of the summer season which follows" (*op. cit.*: 130). The first prebasic molt occurs in *gambeli* from the latter part of April to the latter part of November; molting of the body plumage occurs from the middle of July to the beginning of October (*op. cit.*: 131).

The first prealternate molt occurs "from February to April, or rarely May. . . . The peak of activity occurs in the latter part of February and during March. . . . Whether all birds undergo this molt and whether all individuals molt feathers other than those of the throat, could not be ascertained. At best, the prenuptial [= prealternate] molts are little more than sporadic feather replacements, and the resulting freshening of the normally white throat produces little or no change in appearance" (Miller, 1928: 409).

The second and subsequent prebasic molts are complete. The flight feathers are shed and replaced during the period from the first of July into the first week of October; the body plumage is completely renewed from the last week of July to the middle of October (Miller, 1928: 411). "The period of July, August, and September, during which adult annual [= prebasic] molts have been found to occur is probably a longer period than that required by any one average individual. The previously established mean period of three and one-half months for the incomplete [= first prebasic] molt of first fall birds seems to be at least fifteen or twenty days longer than the probable mean period for adults. . . . adults show more rapid replacement within the different feather groups—adult molts [= prebasic] may be characterized as more vigorous, precise, and rapid than the first fall [= first prebasic] molt" (*op. cit.*: 413).

"Adult annual [= prebasic] molts replace all feathers of the body. But, in first fall birds, only certain feathers being replaced, it would seem logical to suppose that these replacements constitute an adaptation for the purpose of reinforcing the most vulnerable parts of the plumage. Such plumage parts, although not seriously worn at the time of the first fall [= first prebasic] molt, might, if not replaced, reach a dangerous stage of disintegration by the following summer" (*op. cit.*: 414).

The second and subsequent prealternate molts are in all respects similar to the first prealternate molt (*op. cit.*: 409).

SUMMARY

A re-evaluation of the currently accepted terminology of plumages and molts is presented. The significance of the complete "postnuptial" molt as a landmark of plumage equivalence is supported, but the importance of the plumage gained at this molt should be stressed rather than that of the "plumage" lost. The plumage attained at the complete molt may be considered homologous in most birds; other plumages have evolved as additions in response to various types of selection.

A practical terminology is suggested for the description of molts and plumages and for indicating homologies between different groups of birds with respect to patterns of feather replacement. The new

terminology is needed to replace older ones which were semantically dependent on other phenomena.

Existing patterns of feather replacement are enumerated, in order of increasing complexity, from a hypothetical ancestral condition.

Application of the terminology and its use in graphic representation are illustrated, using previously published data on *Calypte anna, Cyanocitta stelleri,* and *Lanius ludovicianus.*

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SEVENTY-SEVENTH STATED MEETING OF A.O.U.

The Seventy-seventh Stated Meeting of the American Ornithologists' Union will take place August 25 to 28, 1959, at Regina, Saskatchewan. Robert W. Nero is Chairman of the General Committee on Arrangements. Chairmen of the subcommittees are: Miss Joyce Dew, Exhibits; Elmer Fox, Finance; Frank H. Brazier, Accommodations and Transportation; Bruce Knox, Meals; Fred G. Bard, Field Trips; Richard W. Fyfe, Publicity; Mrs. John Hodges, Registration; Miss Gertrude Murray, Wives; and James Millington, Visual Aids.